

The last chance to pass the ball: investigating the role of temporal expectation and motor resonance in processing temporal errors in motor actions

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Abstract

Humans can acquire information on others' motor outputs (action prediction) and intentions (action understanding) according to their individual motor repertoire and to the detected gesture's features (e.g. temporal patterns). We aimed at dissociating between action prediction and action understanding abilities in soccer players and novices observing soccer action videos including correct timing pass (CTP) or delayed pass (DP). First, we used an occluding paradigm to evaluate participants' ability to predict the correct time to pass the ball. Although soccer players showed reduced reaction times, all subjects showed a similar pattern of performance: during DP observation, responses appeared delayed with respect to the other conditions but anticipated with respect to the observed DP. In a separate experiment, we investigated the ability to recognize CTP vs DP and the modulation of primary motor cortex (M1) excitability associated to video observation. Only soccer players showed selective modulation of M1 according to the plausibility of the observed action, with increased excitability during the observation of the CTP and in a phase preceding the DP. In conclusion, action prediction ability seems to be independent from the individual motor repertoire. By contrast, only subjects with previously acquired sensorimotor skills are able to infer the observed action's long-term intention.

Key words: action observation network; action prediction; action understanding; motor resonance; temporal expectation; transcranial magnetic stimulation

Introduction

Interaction among individuals in everyday life is often based on movements and gestures. The understanding and prediction of others' actions constitute basic mechanisms of human

relationships and are mediated by a wide range of neural processes in the brain. In particular, changes in the excitability of observers' primary motor cortex (M1) can occur during action observation (AO) (Fadiga *et al.*, 1995; Rizzolatti *et al.*, 1999). This

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phenomenon, known as motor resonance, has been studied during the observation of well-known actions performed with congruent kinematics (Calvo-Merino et al., 2005; Aglioti et al., 2008; Buccino et al., 2013) and in error detection paradigms during the viewing of incongruent movements (e.g. Tomeo et al., 2013; Makris and Urgesi, 2015; Panasiti et al., 2016; Proverbio et al., 2017). However, this research produced non-univocal results, leaving unsolved issues vis-à-vis how the brain processes actions and goals according to their level of abstraction, from the simple visual information of motion to the inference of the long-term intention behind it (Van Overwalle and Baetens, 2009).

To date, motor resonance experiments have been used to index the functioning of the neural network involved during action perception (i.e. the action observation network—AON) (Avenanti et al., 2007, 2013), formed by frontal, parietal, and temporal regions (Gazzola and Keysers, 2009; Grafton, 2009; Caspers et al., 2010). In most of these researches, authors focused on the investigation of intention prediction ability, conferring to the term ‘intention’ a plethora of meanings, from the immediate outcome of an action to the higher-level motivation that produced the action (Wilson and Knoblich, 2005; Kilner et al., 2007; Schütz-Bosbach and Prinz, 2007; Avenanti and Urgesi, 2011). However, it might be of interest to dissociate between ‘action prediction’, i.e. the ability to anticipate an observed action’s outcome (the when of an action), and ‘action understanding’. Action understanding has been defined as the immediate attribution of an intentional meaning to the movement of others (i.e. the why of an action) (Catmur, 2015). It may occur to infer the motor output of others without realizing their final intention. Moreover, action prediction and action understanding may rely on different neural networks and result in different consequences in terms of motor reaction of the observer (e.g. different reaction times).

Furthermore, a modulation of these mechanisms during AO seems to be related to the previous motor experience of the observer. According to this, it has been proposed that an implicit simulation of the observed movement can occur in the onlooker’s motor areas during AO (Rizzolatti and Craighero, 2004; Gallese, 2009; Gallese and Sinigaglia, 2011). This mechanism can be assessed by partially hiding the visual information available to the observer, e.g. by using occluding paradigms (Avanzino et al., 2013; Martino et al., 2015). When subjects are required to estimate the hidden part of the action, they need to implicitly extract temporal patterns and regularity of events in order to synchronize the motor response to a strict temporal framework (i.e. temporal expectation) (Nobre et al., 2007; Coull and Nobre, 2008; Bove et al., 2017). This is a frequently used expedient to test motor prediction ability according to individual motor repertoires and, by integrating unexpected or inconsistent actions (e.g. temporal errors), may enable reproducing real-world situations, providing new insights in a growing area of social neuroscience, as suggested in a recent meta-analysis (Van Overwalle and Baetens, 2009).

A suitable model to investigate these aspects is represented by open-skill sports. Indeed, athletes need to predict the effects of others’ actions from the beginning of the gesture (Smith, 2016), infer opponents’ and teammates’ intentions and plan a proper motor response, activating the whole hierarchical representation of motor perception. Moreover, specific game situations may limit the visual information available to the players, engaging temporal expectation mechanisms. In this context, temporal feature processing plays a crucial role in action prediction and understanding, and individual motor repertoires might influence these abilities.

In our opinion, the following questions may need an answer: How is action prediction influenced by observed temporal errors, according to individual motor expertise? What happens in the brain when a movement does not occur in the instant in which it was expected? What happens if it occurs in a delayed phase of the observed action?

The present work aimed at dissociating the mechanisms used to predict others’ motor outputs (action prediction) and to infer the intentional meaning of the observed actions (action understanding). To this end, two different experiments were designed, involving soccer players and novices while observing soccer actions differing only in the time of movement execution (here, a pass between two players): temporal expectation and motor resonance mechanisms were investigated in two different experiments. We firstly applied an occluding paradigm to investigate the ability to temporally predict the correct time when the ball had to be passed by a soccer player to a sprinting teammate in soccer action videos. Some video clips included a delay in the pass execution in order to study its influence on temporal expectation performance. We wondered if previously acquired sensorimotor skills influence the ability to predict the correct time of the pass without being influenced by the delay in the observed action. Furthermore, we explored M1 excitability and cortical inhibition during the discrimination of the same correct and delayed actions by means of transcranial magnetic stimulation (TMS). Following the assumption that AON matches the perceived actions to a representation of the observers’ own actions depending on their motor experience (Calvo-Merino et al., 2005; Cross et al., 2006), we hypothesized that M1 excitability in soccer players increased during the observation of correct passes. Further, similar increases in M1 excitability could be expected during the observation of the delayed video at the time the pass should have been performed. At the same time, changes in the excitability of cortical inhibitory circuits could be postulated when observing unexpected (delayed) actions, according to the notion that intracortical networks would shape the motor resonance mechanism (Strafella and Paus, 2000; Koch et al., 2010).

Materials and methods

Participants

Seventy-two volunteers (30 females and 42 males) aged 18–40 years (mean \pm standard deviation [s.d.] = 23.6 \pm 3.9 years) participated in the study. The following criteria were considered for inclusion: reported right foot dominance, no previous history of neurological disorders, no recent orthopaedic problems for the right-dominant foot, no contraindications to TMS and normal or corrected-to-normal vision.

All 72 participants completed a questionnaire giving brief demographic details and providing information on their soccer experience. Based on the answers given, subjects were classified as soccer players or as novices. In particular, in line with a previous study (Wright et al., 2013), skilled players were defined as those playing currently or within the last year for a club registered in the Italian Soccer Federation (Federazione Italiana Giuoco Calcio, FIGC) local league. Conversely, novices were defined as people who had never played soccer or people with only recreational experience concluded more than 1 year previously. Moreover, they did not regularly watch soccer matches.

Soccer players and novices were assigned to one of two separate experiments: 20 soccer players (Soccer_Exp1) and 20 novices (Novice_Exp1) participated in a behavioural experiment (Experiment 1), investigating temporal prediction ability, while

Table 1. Comparison of demographics and soccer experience of the participant groups

Group	Age ^a (years)	Gender ^b (M/tot)	Years played ^c	Hours of training per week ^c
Soccer_Exp1	23.3 ± 4.7	14/20	14.6 ± 4.8	4.7 ± 2.2
Novice_Exp1	25.7 ± 3.9	8/20	0.3 ± 1.3	0.0 ± 0.0
	$t = 1.75$	$\chi^2 = 3.64$	$U = 1.0$	$U = 30.0$
	$P = 0.09$	$P = 0.06$	$P < 0.0001$	$P < 0.0001$
Soccer_Exp2	22.5 ± 3.4	12/16	11.0 ± 6.3	3.6 ± 3.0
Novice_Exp2	22.4 ± 1.9	8/16	0.2 ± 0.7	0.0 ± 0.0
	$t = 0.06$	$\chi^2 = 2.13$	$U = 0.0$	$U = 24.0$
	$P = 0.95$	$P = 0.14$	$P < 0.0001$	$P < 0.0001$

Mean ± s.d. of participants groups are reported.

^aDemographics were compared by means of the Student's t-test for independent samples.

^bDemographics were compared by means of the chi-squared test.

^cSoccer experience was compared by means of the Mann-Whitney U test.

16 soccer players (Soccer_Exp2) and a matched novice group (Novice_Exp2) participated in a neurophysiological study of M1 excitability modulation (Experiment 2). Demographics and soccer experience of the groups are reported in Table 1.

In Soccer_Exp1, 17 out of 20 subjects were currently playing soccer, while 3 participants had stopped in the previous year. In Novice_Exp1, only one subject had previous recreational soccer experience. Twelve subjects included in Soccer_Exp2 were currently playing soccer and four had stopped playing in the previous year, whilst only one subject included in Novice_Exp2 had previous recreational soccer experience. It is worth noting that the mean number of soccer matches watched by subjects recruited in this study as novices was very low (0.56 ± 1.11 matches per month). Neither in Experiment 1 nor in Experiment 2 did the two groups differ significantly concerning age or gender, whilst they significantly differed in soccer experience. Moreover, the two soccer player groups did not differ in age ($t = 0.605$, $P = 0.549$), gender (chi-squared = 0.111, $P = 0.739$), years of soccer experience ($U = 98.5$, $P = 0.06$) or number of hours of training per week ($U = 125.0$, $P = 0.26$).

The experimental design was approved by a local ethics committee and was carried out in agreement with legal requirements and international norms (Rickmap, 1964). All participants gave their informed consent to participate in the study.

Experimental design

Videos. In both Experiment 1 and Experiment 2, the same videos representing a soccer action with different spatiotemporal patterns were used.

Videos were recorded during soccer actions performed by athletes recruited from a sports science degree programme (University of Genoa, Italy). Actions showed an athlete playing in the role of midfielder receiving the ball and performing a pass to a teammate in the role of winger sprinting towards the goal (Figure 1). The midfielder was instructed to perform the pass with either a correct or a delayed timing with respect to the teammate's movement. Among the recorded actions, two videos were selected according to the following criteria: (i) they should include a correctly timed pass (CTP video) and a delayed pass (DP video); and (ii) the other spatiotemporal features (e.g. the winger run, the trajectory of the ball) should not differ between videos.

Experiment 1. During the experiment, participants sat in a dimly lit room in front of a 15-inch monitor (resolution, 1366×768 pixels; refresh frequency, 60 Hz) positioned 80 cm away from the subject, in which videos were presented on a black background.

From the original videos, we created six new clips (three from CTP video and three from DP video) in which the passing midfielder's movements were occluded at different instants by means of a dark window occluding the left half of the screen (Figure 2). In particular, the videos were occluded at: (i) 1100 ms after the beginning of the videos, corresponding to 500 ms after the initial pass in the action, executed by a third player towards the midfielder (Pass_0). The observer was able to see the initial development of the action, whilst information concerning the midfielder's movements and related pass timing were occluded early (i.e. before he received the ball) (Early_Occl condition); (ii) 1850 ms after the beginning of the videos, corresponding to the time at which the midfielder received the ball. The observer could see the early movements of the midfielder, but his postural adjustments after he received the ball and the consequent pass timing were occluded (Mid_Occl condition); and (iii) 3900 ms after the beginning of the videos. In this condition, the observer could see the entire midfielder movements from the early phases of postural adjustments until the execution of either the correct or the delayed pass (Late_Occl condition).

The six new clips were randomly presented to subjects, and participants were asked to press a key button when they considered the pass should have been performed based on the sprinting winger's run. They were instructed to focus the gaze on the midfielder but to press the button independently from his behaviour and from the onset of the occluding window. Before the beginning of the experiment, subjects watched the CTP video without occlusions in order to see the entire action and understand its development.

Each video clip was presented to subjects 15 times, for a total of 90 repetitions of video presentation. Additionally, to keep participants attentive to the visual stimulus, a static image representing a cross (+) was presented instead of the video for 10 pseudorandomly distributed repetitions, and participants were asked to update the count of them (Bisio et al., 2017). At the end of the session, the experimenter asked for both the number of crosses counted and the number of different actions observed in order to exclude stereotyped responding given by the realization that all stimuli were based on the same two videos (i.e. CTP and DP).

A total of 100 stimuli (90 videos and 10 static crosses) was presented in pseudorandom order in four blocks (25 stimuli each). A resting time of about 2 min was allowed between blocks.

E-Prime version 2.0 software (Psychology Software Tools Inc., Pittsburgh, PA) was used to randomize and present the

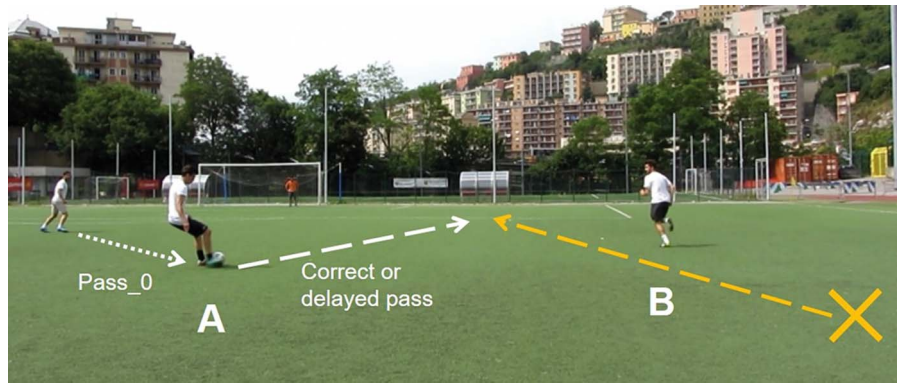


Fig. 1. Video frame showing the soccer action scenario. The videos represented a soccer action consisting of a pass performed by an athlete playing in the role of midfielder (A) to a sprinting teammate (B). Midfielder A received the ball from a third player (Pass_0, dotted white arrow) and performed the pass (dashed white arrow) to the winger B, sprinting toward the goal (yellow arrow). The pass could be performed with either correct or delayed timing with respect to the teammate's movement.

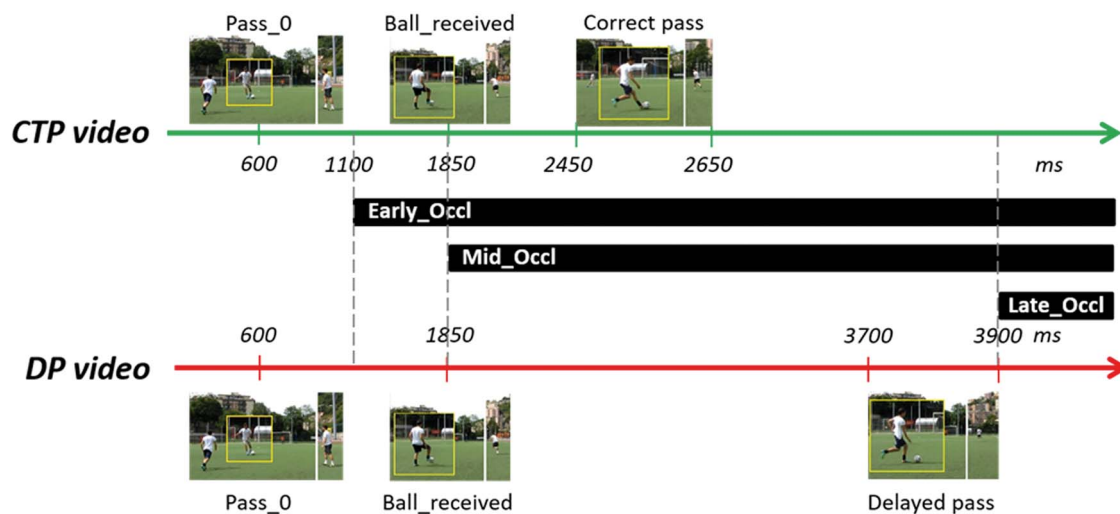


Fig. 2. Design of Experiment 1. Both correct timing pass (CTP) and DP videos were occluded in the left part of the screen at three different time points (i.e. occluding the midfielder's movements for different time intervals). Thus the occluding window appeared with three possible onset times: an early phase of videos, when only the initial action developing was visible in its entirety (Early_Occl); a mid-phase of videos, when the midfielder's early movements but not his subsequent postural adjustments were visible (Mid_Occl); and a late phase of videos, when observers could see the midfielder's movements from early phases until the execution of either correct or delayed pass (Late_Occl condition).

stimuli and to record participants' responses. Outliers (i.e. trials exceeding ± 2 s.d. from the subject's mean for each experimental condition) were excluded from the analysis.

Experiment 2. In Experiment 2, participants sat with their knees and ankles flexed at 90° in a comfortable chair in a quiet room, 80 cm away from a monitor where videos were displayed. During video observation TMS pulses were administered to assess M1 activity according to the protocol described below; moreover, after each video, subjects were asked to judge the appropriateness of the observed pass in a scale ranging from 1 (bad pass) to 10 (excellent pass). This allowed probing subjects' ability to immediately attribute an intentional meaning to the observed movement (i.e. action understanding), here to perform a correct-timing pass in order to assist the teammate.

Motor evoked potentials (MEPs) were recorded from the right tibialis anterior (TA) since it is a muscle involved in the soccer pass movement. Electromyographic signals (EMG) were recorded using silver disc surface electrodes taped to the belly and tendon of the muscle. The ground electrode was placed over the knee. EMG were digitalized, amplified and filtered (20 Hz–1 kHz) with a

1902 isolated preamplifier controlled by the Power 1401 acquisition interface (Cambridge Electronic Design Limited, Cambridge, UK) and stored on a personal computer for display and later offline data analysis.

Single-pulse TMS was performed by means of a double cone coil connected to a single Magstim 200² magnetic stimulator (Magstim Co Ltd, UK). During the recording session, the coil position was centred approximately over the vertex and moved in 1-cm steps around the lower limb area of the left motor cortex in order to detect the optimal scalp position, defined as the position from which MEPs with maximal amplitude were recorded from TA at constant TMS pulse intensity. TMS was administered using posterior-anterior currents to the brain. Then, we determined the active motor threshold (AMT), defined as the minimum amount of machine output necessary to elicit a clear motor response in 5 out of 10 TMS pulses during a minimal voluntary contraction. Stimulation intensity was then set at 150% of the AMT for all subjects.

During the recording session, participants were asked to slightly contract the TA. To have a comparable facilitation

throughout the experiment, a measure of the maximum voluntary isometric contraction (MVIC) was obtained from TA muscle before the TMS measurement. Subjects performed two consecutive MVICs against a resistance produced by the experimenter and then were trained to match a target contraction corresponding to 30% MVIC by means of real-time visual feedback. The recording session started only when subjects were confident with the target facilitation contraction (i.e. when they could produce 30% MVIC accurately), and during video presentation they had to reproduce a sequence of brief 30% MVIC contractions initiating at the 'start' signals given by the experimenter and terminating at the end of each observed video.

This allowed us to measure the duration of the contralateral silent period (cSP), calculated as the amount of time between the cSP onset (time where the EMG signal returned to the baseline after the MEP) and the cSP offset (return of the voluntary contraction) (Houde et al., 2018). Although the initial portion of cSP is primarily due to spinal mechanisms (Chen et al., 1999), several studies established that its late part reflects a cortical origin (Chen, 2004; Kimiskidis et al., 2005) mediated by GABAergic receptors within M1 (Ziemann et al., 1996). Thus, cSP duration is often used as a measure of excitability in cortical inhibitory circuits (Orth and Rothwell, 2004).

A MatLab custom-made software managed stimuli presentation and TMS triggering. TMS was delivered at specific time points in order to evaluate M1 excitability and cortical inhibition during different AO conditions, with particular focus on possible mechanisms of motor resonance elicited by the observation of temporally correct and incorrect actions in soccer players and novices. Thus, three stimulation instants were defined for each video, according to action development. In the first condition, TMS was synchronized in order to release a pulse at the time of the midfielder's correct pass in the CTP video. Indeed, it has been shown that the activity of the motor cortex changes as a function of the action's phase and reaches its maximum when the muscle involved in the observed action is active (Bisio et al., 2015). Thus, the instant of the contact between the foot and the ball was chosen (i.e. 2650 ms), since it was demonstrated that TA activation reaches a peak (>85% MVIC) in the phases shortly preceding the side-foot kick (Brophy et al., 2007). This time point corresponded to the early phase of the winger's run in both videos (Early_run). Another stimulation condition was set at the time the ball was passed in the DP video (i.e. 3900 ms), corresponding to the final part of the winger's run in both videos (Late_run). Moreover, an intermediate stimulation time point was set in order to investigate the modulation of M1 activity during the observation of a phase when the pass could have been performed, according to the development of the action (i.e. the sprinting winger's movement), but was not (in the case of DP video). Thus, the instant of this stimulation time point was set following the averaged responses given by participants of Experiment 1, who were asked to press the button when they considered the pass should have been performed. In detail, the mean response time for both Soccer_Exp1 and Novice_Exp1 recorded in Late_Occl condition of the DP video was set as the stimulation time point for Experiment 2 and corresponded to the halfway phase of the winger's run in both videos (i.e. 3250 ms, Half_run). The TMS paradigm is represented in Figure 3.

TMS pulses were also administered during the observation of a static cross in order to provide baseline values of M1 excitability and cortical inhibition for each participant. The baseline condition was recorded before the experimental blocks in order to obtain unbiased measurements (Labruna et al., 2011), and

participants were requested to activate the TA muscle like during video observation.

The protocol included 90 trials: 10 MEPs and cSPs were recorded for each experimental condition given by the combination of stimulus (baseline, CTP video or DP video) and TMS time point (Early_run, Half_run and Late_run). Trials were pseudorandomly divided in 3 blocks of 30 trials each, separated by a 2-min resting interval. An intertrial interval of 10–15 s was scheduled in order to avoid muscular fatigue throughout the experiment. In order to exclude outliers, trials showing peak-to-peak values of background EMG exceeding ± 2 s.d. from the subject's mean were not considered for analyses. In this contingency, new records of the corresponding experimental conditions were added at the end of the experiment in order to collect 10 records with homogeneous pre-stimulus EMG activity. Post-processing also included root-mean-square (RMS) evaluation of the pre-stimulus EMG (90 ms before TMS) to control for an influence of background activity on MEP amplitudes and cSP durations.

As in Experiment 1, participants were asked to focus the gaze on the midfielder, and, at the end of the TMS session, we assessed whether the subjects recognized the repetition of the same videos by asking them to evaluate the number of different actions observed (i.e. two: CTP and DP).

Statistical analysis

Demographic data of the participant groups were compared by means of Student's t-test for continuous variables (age) and chi-squared test for categorical variables (gender). Groups' soccer experience was compared with Mann-Whitney U tests since both years of practice and hours of training violated normality (Shapiro-Wilk $W=0.75$, $P<0.0001$, and $W=0.69$, $P<0.0001$, respectively).

For Experiment 1, individual estimates of the percentage of crosses seen were compared between groups (Mann-Whitney U test).

Concerning Experiment 1, participants' response time data were entered in an analysis of variance (ANOVA) with GROUP (two levels: Soccer_Exp1 and Novice_Exp1) as between-subjects factor and VIDEO (two levels: CTP and DP videos) and OCCLUSION (three levels: Early_Occl, Mid_Occl and Late_Occl) as within-subjects factors.

In Experiment 2, scores attributed to CTP and DP videos have been compared between groups using the Mann-Whitney U test. With regard to neurophysiological data, we tested background EMG similarity across conditions with an ANOVA on RMS values. Then, MEPs' peak-to-peak amplitude (in millivolts) and cSP duration (in milliseconds) have been calculated and analysed offline in terms of normalized values, resulting from the ratio between the mean value recorded during the video presentation (CTP and DP videos) and during the baseline condition (cross observation). Normalized data were entered in an ANOVA that included GROUP (two levels: Soccer_Exp2 and Novice_Exp2) as between-subjects factor and VIDEO (two levels: CTP and DP videos) and TIME in which TMS was delivered (three levels: Early_run, Half_run and Late_run) as within-subjects factors.

Moreover, in order to probe the absence of confounding effects, MEPs' amplitudes elicited at the three different time points (Early_run, Half_run and Late_run) of baseline condition have been compared between groups by means of an ANOVA.

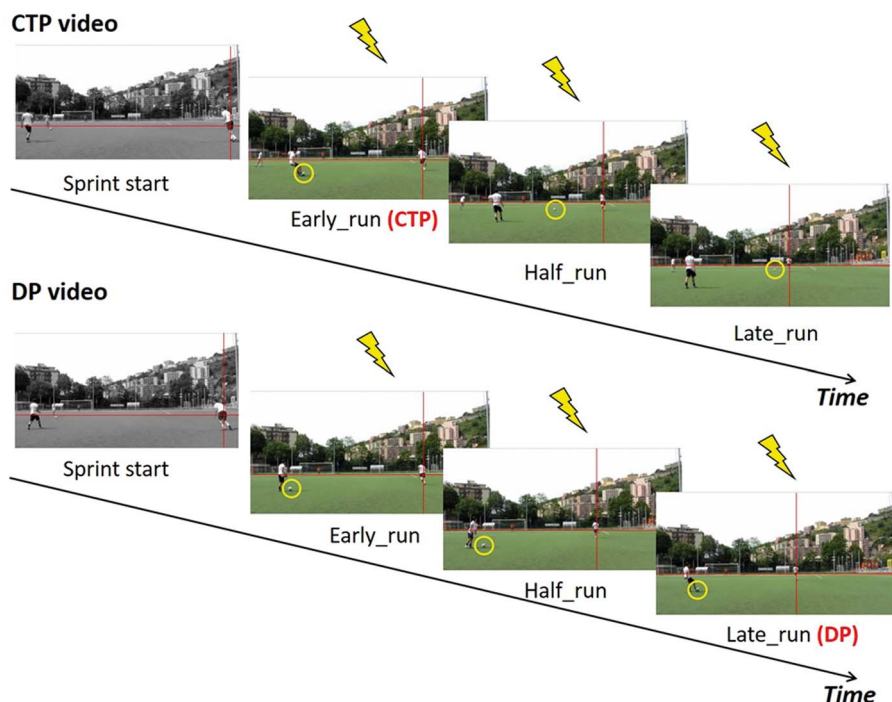


Fig. 3. Design of Experiment 2. TMS pulses were administered at one of three different time points during the observation of the videos. In particular, stimulation occurred in the early phase (Early_run), halfway phase (Half_run) or late phase (Late_run) of the winger's run. Concerning the CTP video, Early_run corresponded to the instant the pass was performed, whilst for the DP video, the pass occurred at Late_run. Importantly, the stimulation time points were set at similar stages for the two videos with regard to action development, as shown by the position of the sprinting winger, highlighted by the red markers in the figure. Yellow circles identify the ball position at the different time points of the CTP and DP videos.

Significant main effects ($P < 0.05$) were further investigated by means of the least significance difference (LSD) of Fisher post hoc test.

Results

In both experiments, all participants estimated the number of different actions observed as higher than five, indicating that they were not able to detect the repetition of the same two video clips and suggesting that individuals' responses were based on 'kinematic reading' and not on other abilities such as memory.

Experiment 1

Both groups accurately reported the number of crosses appearing during the experimental session (98.75 and 96.67% of correct answers for Soccer_Exp1 and Novice_Exp1, respectively; $U = 168.5$, $P = 0.241$).

ANOVA on subjects' response times revealed a significant main effect of GROUP ($F_{1,38} = 4.359$, $P = 0.044$, $\eta^2 = 0.103$), VIDEO ($F_{1,38} = 29.544$, $P < 0.0001$, $\eta^2 = 0.437$) and OCCLUSION ($F_{2,76} = 54.718$, $P < 0.0001$, $\eta^2 = 0.590$).

In particular, Soccer_Exp1 responded earlier (2608.74 ± 479.74 ms) with respect to Novice_Exp1 (2879.34 ± 563.62 ms) ($P = 0.043$). As shown in Figure 4A and B, when observing the CTP video, Soccer_Exp1's mean response time was included within the time interval corresponding to the correct pass in all occlusion conditions, whilst Novice_Exp1 responded with a delay.

Irrespective of the amount of information captured by the observed video (i.e. in any occlusion condition), during DP video subjects responded later than during CTP video ($P < 0.0001$). As well, later occlusion induced delayed

responses (Late_Occl > Mid_Occl and Early_Occl: $P < 0.0001$; Mid_Occl > Early_Occl: $P = 0.001$).

Concerning interactions among factors, a significant effect of VIDEO \times OCCLUSION ($F_{2,76} = 49.26$; $P < 0.0001$, $\eta^2 = 0.565$) was found. Post hoc analysis revealed that response time in Late_Occl condition during the observation of DP video differed from all other conditions ($P < 0.0001$). It is important to note that although a delayed pass was presented to the observers in this condition, subjects pressed the key button before the midfielder executed the delayed pass, anticipating the movement they actually observed.

No other significant interactions were found between GROUP and VIDEO and GROUP and OCCLUSION nor GROUP, VIDEO and OCCLUSION (all P s > 0.05).

Experiment 2

The two groups differently judged CTP (Soccer_Exp2: 8.52 ± 0.89 ; Novice_Exp2: 7.57 ± 1.18 ; $U = 63$, $P = 0.014$, $\eta^2 = 0.400$) and DP (Soccer_Exp2: 2.36 ± 1.27 ; Novice_Exp2: 3.67 ± 1.83 ; $U = 73$, $P = 0.038$, $\eta^2 = 0.287$) videos. Indeed both groups of participants gave higher scores to the CTP than the DP video, suggesting a judgment of better quality of the pass for the CTP video. Interestingly, soccer players gave higher scores than novices to the CTP video and lower scores than novices to the DP video, indicating higher discriminating ability.

Participants' MVIC did not differ between groups (mean Soccer_Exp2 = 3.91 ± 1.14 mV; mean Novice_Exp2 = 3.32 ± 1.23 mV; $t = 1.39$; $P = 0.17$), and background EMG activity was similar across conditions during the experiment (Table 2). The ANOVA on RMS values showed no significant interaction among factors GROUP \times VIDEO \times TIME ($F_{2,60} = 0.12$, $P = 0.89$).

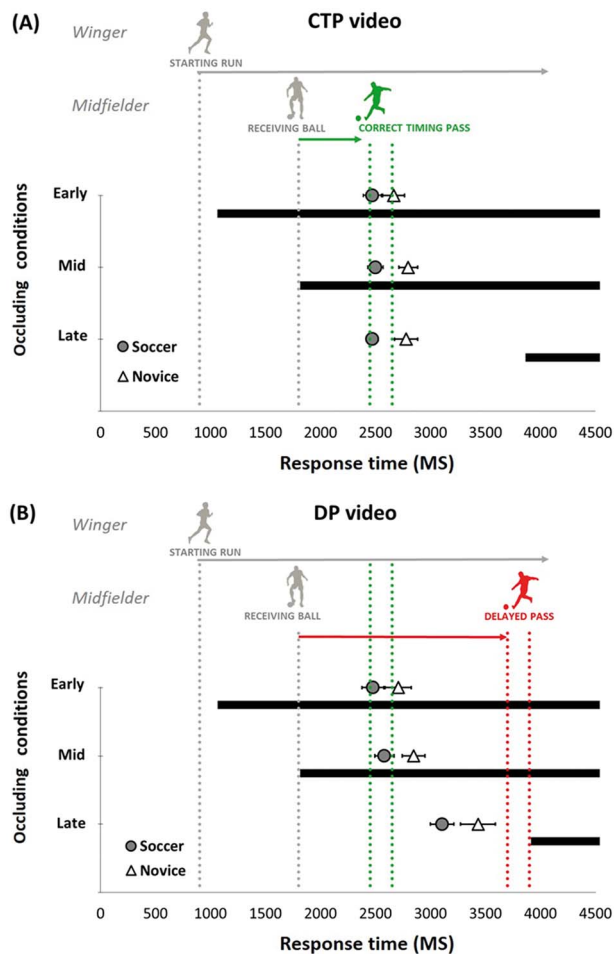


Fig. 4. Results of Experiment 1. When observing CTP video (A), soccer players responded within the temporal range that the correct pass was executed in all occlusion conditions (grey circles in A). Conversely, novices responded with a delay with respect to soccer players (white triangles in A). When observing the DP video (B), both groups showed response times similar to the CTP video in early and mid occlusion conditions (i.e. when the temporal error of the midfielder was occluded), whilst they delayed the response in Late_Occl condition. Green lines represent the time interval of CTP kicking motion (from the right toe off to the ball impact, as defined by Nunome et al., 2002). These were reported also in the graph of DP video in order to easily collocate when the pass should have occurred with respect to the winger run. Red lines represent the time interval of DP kicking motion.

With regard to MEP amplitude changes, we found a statistically significant main effect of TIME ($F_{2,60} = 4.531, P = 0.015, \eta^2 = 0.131$) and of the interaction between GROUP, VIDEO and TIME ($F_{2,60} = 4.621, P = 0.014, \eta^2 = 0.133$). In particular, TMS pulses administered in the later phase of the videos (Late_run) elicited lower MEPs with respect to the Early_run ($P = 0.037$) and Half_run (0.005) time points. However, post hoc analysis of the significant three-way interaction revealed that only Soccer_Exp2 showed a modulation of cortical excitability. Indeed, when observing CTP video (Figure 5A), Soccer_Exp2 showed significantly higher normalized MEPs at the moment in which the ball was passed (Early_run) with respect to the subsequent time points (Half_run, $P = 0.026$ and Late_run, $P = 0.003$), whilst no significant difference in MEP amplitude was found between Half_run and Late_run conditions ($P = 0.431$). Instead, when observing the DP video (Figure 5B), M1 excitability of soccer players was higher in correspondence to Half_run, i.e. when the pass had not yet been executed, with respect both to Early_run ($P = 0.004$) and also

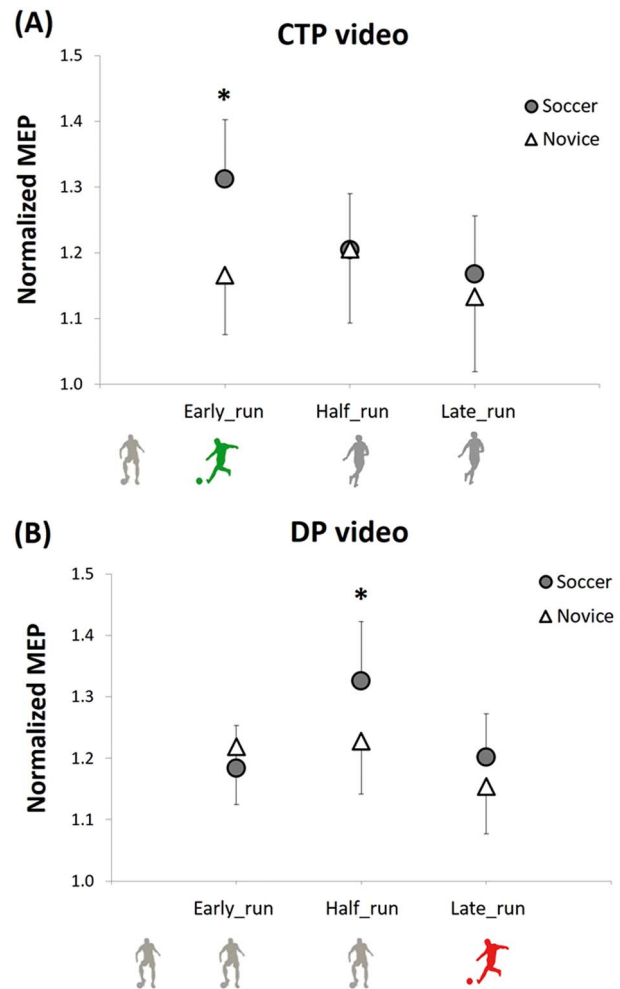


Fig. 5. Results of Experiment 2—MEP. M1 excitability is modulated by different spatiotemporal features of the observed action in soccer players but not in novices. In detail, during the observation of the correct timed video (A), Soccer_Exp2 showed higher activation when observing the pass (Early_run) with respect to the other conditions. On the other hand, during the observation of the delayed video (B), soccer players showed higher M1 excitability before the execution of the pass (Half_run), whilst they showed lower MEP amplitude during the observation of the delayed pass (Late_run). Novice_Exp2 did not show any modulation of M1 excitability either during the CTP or DP video. MEP values are reported as normalized with respect to baseline measures. Bars indicate standard errors. * refers to significant differences between conditions and within the group ($P < 0.05$).

to Late_run ($P = 0.011$), corresponding to the delayed pass time execution. Here, no significant difference of MEP amplitude was found between Early_run and Late_run conditions ($P = 0.710$).

By contrast, Novice_Exp2 did not show any significant modulation of M1 excitability during the observation of either CTP or DP video.

No main effect of GROUP and VIDEO nor two-way significant interactions between GROUP and VIDEO and GROUP and TIME nor VIDEO and TIME were observed (all $P_s > 0.05$).

Analyses of normalized cSP showed a significant increase of cSP duration during Late_run than during Half_run and Early_run (main effect of TIME: $F_{2,50} = 12.456, P < 0.0001, \eta^2 = 0.462$) and during the observation of DP with respect to CTP video (main effect of VIDEO: $F_{1,25} = 7.648, P = 0.010, \eta^2 = 0.203$). However, we also found a significant effect of GROUP \times VIDEO ($F_{1,25} = 6.795, P = 0.014, \eta^2 = 0.185$). Post hoc analysis of this interaction revealed that the increase of cSP duration during DP video with respect

Table 2. Background EMG activity of soccer players and novices across the different experimental conditions

	CTP			DP		
	Early_run	Half_run	Late_run	Early_run	Half_run	Late_run
Soccer_Exp2	0.19 ± 0.04	0.17 ± 0.04	0.17 ± 0.05	0.19 ± 0.05	0.18 ± 0.05	0.17 ± 0.05
Novice_Exp2	0.16 ± 0.06	0.16 ± 0.06	0.16 ± 0.05	0.16 ± 0.06	0.17 ± 0.07	0.16 ± 0.05

RMS mean ± s.d. values (mV) of pre-stimulus EMG (90 ms before TMS) are reported for CTP and DP videos and the three TMS time points (Early_run, Half_run and Late_run).

to CTP video observation was significant only in Soccer_Exp2 ($P=0.002$) and not in Novice_Exp2 ($P=0.930$) (Figure 6). No effect of GROUP, GROUP × TIME, VIDEO × TIME nor GROUP × VIDEO × TIME on cSP duration was found (all $P_s > 0.05$).

Further, the ANOVA performed on the baseline condition revealed that MEP amplitude was not influenced by factors other than AO (GROUP, TIME of TMS and two-way interaction were not significant; all $P_s > 0.05$).

Discussion

In this work, we dissociated action prediction from action understanding, demonstrating that these abilities seem to be differently mediated by the AON in accordance with the previously acquired sensorimotor skills.

In the temporal expectation task, we found a main group difference, suggesting that soccer players were better able to predict the execution of a motor output following an event (here, the teammate's sprint) than novices. However, both groups showed consistent responses throughout the occluding paradigm. Only in the delayed pass (DP) condition with late occlusion, subjects delayed their responses as they were influenced by the delay in the observed action. It is worth noting that they responded before they observed the pass execution, implying that all participants were able to temporally predict the event. This suggests that both soccer players and novices could infer the timing in which an event should occur using high-level cognitive functions, such as attentional and visuospatial strategies based on generalized experience.

Contextually, the selective modulation of cortical activity shown by soccer players in Experiment 2 suggests that a more pronounced activation of the motor system, possibly through an implicit simulation of the observed action, might occur in soccer players, contributing to this group's finer ability in CTP vs DP discrimination and faster reaction times. During the CTP video, they showed increased excitability when observing the pass execution, in line with the motor resonance theory, whilst during the DP video, they showed an increase of M1 activity in a phase preceding the pass (which, in this case, was inappropriate because delayed with respect to the context). Surprisingly, cortical excitability did not increase during the observation of the delayed pass, suggesting that soccer players not only showed a phase-specific modulation of corticospinal excitability (Gangitano et al., 2001) but also overlapped their own expectation of the appropriate action, resulting in increased M1 activity when the movement should have been performed, even in the absence of perceived movements. Furthermore, in accordance with neurophysiological findings, soccer players were more precise than novices in discriminating CTP vs DP videos when asked to verbally judge the quality of the pass, corroborating the hypothesis of a relation between action understanding and motor resonance.

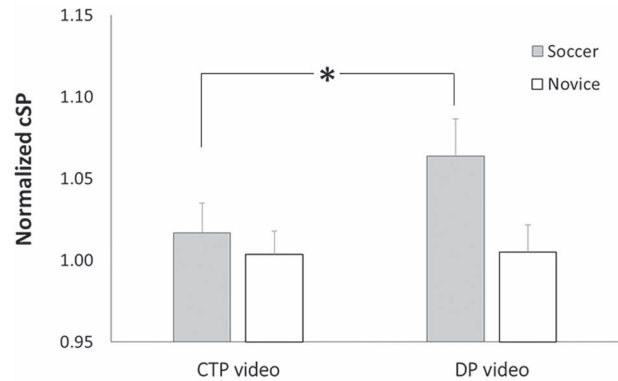


Fig. 6. Results of Experiment 2—cSP. Cortical inhibition increased in soccer players during DP video observation, whilst it did not change in novices. cSP duration values are reported as normalized with respect to baseline measures. Bars indicate standard errors. * refers to significant differences between conditions and within the group ($P < 0.01$).

Action prediction

Results of the temporal expectation task showed that soccer players anticipated their responses with respect to novices in all occlusion conditions. This finding highlights that the ability to extract temporal patterns from a motor action is influenced by familiarity with the gesture. This is in line with previous research showing that the ability of athletes to acquire excellent aptitude in perceiving and performing fast and complex actions in the space-time domain is strongly related to the sports training programme (Bootsma and van Wieringen, 1990; Bove et al., 2017; Causer et al., 2017). Studies focusing on explicit timing mechanisms have demonstrated that task duration knowledge and skill level are involved in time perception, as measured by time estimation and production tasks in swimmers and runners (Tobin and Grondin, 2012, 2015). In our study, we added the concept that sensorimotor skills acquired during extensive training such as athletes do with their sport exert an influence also in implicit timing mechanisms.

Unexpectedly, despite the above discussed group difference, response trends were similar in soccer players and novices, i.e. both groups delayed their response when observing a temporal error but anticipated it with respect to the seen action. This could suggest that all participants were able to temporally predict the action observed. This ability relies on the AON and, in particular it was associated with the anterior intraparietal sulcus (Hamilton and Grafton, 2006), which could be linked to higher-level cognitive functions (e.g. visuospatial processing or motor memory), allowing both skilled subjects and novices to perform this task.

M1 excitability and cortical inhibition

AO elicited an activation of the motor system in all subjects, in line with the evidence documented in the literature (see Fadiga

et al., 2005 for a review). However, novices did not show any M1 excitability difference across the experimental conditions but only a non-specific effect of the observation of moving stimuli. Similar results were found in a previous study (Aglioti et al., 2008), in which novices presented generic motor system activation independently of the stimulus observed, either a free shot in basketball or a soccer kick. Here, the general motor system activation is elicited by the same movement independently of the different temporal pattern presented, suggesting that this behaviour is transversal to the dimension investigated, either kinematic or temporal.

By contrast, when observing the CTP video, soccer players showed the highest cortical facilitation in the *Early_run* condition, i.e. when the midfielder passed the ball to the winger. Moreover, we found a reduction of M1 excitability towards the baseline value after the action was performed. In accordance with these results, previous studies have shown that during AO, onlookers use specialized motor representations to understand the seen actions (Calvo-Merino et al., 2006). Indeed, familiarity with the perceived movement modulates activation of the AON (Calvo-Merino et al., 2005; Fiorio et al., 2010), suggesting that the observation of actions involves matching the individual's motor repertoire and not only a perceptual template.

Furthermore, when the pass was performed with a time delay (i.e. in the DP video), soccer players showed the highest M1 excitability values in the *Half_run* condition and not in the *Late_run* condition, during which the pass was actually performed. This result can be explained as the ability of the motor system to temporally simulate an action in the instant in which it is still meaningful and not in the subsequent time span, i.e. to predict the last chance the player has to pass the ball.

This concept is supported by previous evidence showing that skilled subjects present decreased M1 excitability when observing fooling actions (Tomeo et al., 2013). In their work, the authors investigated corticospinal reactivity of expert kickers, goalkeepers and novices watching manipulated videos representing soccer penalty kicks so that the congruence between the model's body kinematics and the subsequent ball trajectory was altered. Lower motor facilitation for incongruent actions was found among goalkeepers, suggesting that the update of simulative motor representations of others' actions facilitated by expertise resulted in the inhibition of the motor system when observing fooling actions. Our findings demonstrate that in skilled subjects a decrease of M1 excitability can be induced not only by incongruent and/or erroneous actions but also by correct gestures and congruent consequent outputs (here, the pass trajectory) if they are executed with incorrect temporal patterns.

In addition, the increased cortical inhibition that soccer players presented during DP video observation with respect to novices indicated that cSP duration may represent an additive marker of action perception. In particular, increased inhibitory activity in M1 during the observation of erroneous movements may provide evidence of deeper action understanding, as a mechanism occurring in order to suppress imitation (Brass et al., 2001).

Moreover, specific inhibition of the motor system has been associated with self-representation (Schütz-Bosbach et al., 2009), corroborating our hypothesis of stronger activation of simulation processes adopted by experts to anticipate, predict and understand the others' movement.

This evidence suggests that cortical suppression for actions linked to the self might prevent inappropriate perseveration within the motor system.

Temporal expectation, motor resonance and action understanding

Electrophysiological recordings in monkeys have shown that neural firing varies dynamically as a function of the conditional probability that a target will occur at a particular time, given that it has not already occurred (the 'hazard function') (Coull and Nobre, 2008). In humans, during a choice reaction-time task, increased activity was observed in the parietal cortex and cerebellum as a feature of the hazard function (Martin et al., 2008). Several studies have demonstrated that temporal expectation is represented within areas traditionally associated with action, notably premotor or inferior parietal cortices (Coull and Nobre, 2008). Activation of action-related areas by perceptual temporal expectation is consistent with the observation that motor areas can code for perceptual representations of action as well as their actual execution (Rizzolatti and Craighero, 1998), suggesting that the main goal of temporal expectation is to optimize prospective motor behaviour. The inference about the time when an event should occur seems to be mainly associated with the inferior intraparietal sulcus and linked to visuospatial processing and motor memory (Hamilton and Grafton, 2006). Moreover, we could suggest that it is independent from the individual sensorimotor repertoire: indeed, in Experiment 1, during DP video observation, both soccer players and novices pressed the button before the pass was really executed, showing similar action prediction ability.

By contrast, only previously acquired specific sensorimotor skills allowed soccer players to infer the observed action's intention, which in this study was to perform a pass to the sprinting teammate with appropriate timing. This ability seems to be tightly associated to the AON and its components: (i) the premotor cortex (Hamilton and Grafton, 2008), which could be responsible for the increased M1 excitability observed in our study; (ii) the inferior frontal cortex, which was shown to be necessary for predicting the outcomes of observed human actions (Avenanti et al., 2018); and (iii) M1 itself, as it demonstrated its pivotal role in selectively predicting human but not non-biological motor outputs (Paracampo et al., 2018).

Considered together, these evidences suggest that action understanding (i.e. why a movement should be performed) is based on motor resonance. Consistently, the higher M1 excitability shown by soccer players in the *Half_run* condition than in the *Late_run* condition, during which the pass was really performed (DP video), could suggest that temporal aspects of the subjective motor repertoire can be influenced by the AON not only in the process of movement recognition but also in the predictive coding process in terms of temporal organization. Indeed, it is worth noting that our motor repertoire includes several over-learned movements, which are well characterized in terms of temporal organization, and that during AO the temporal properties of a movement are recognized (Gavazzi et al., 2013; Avanzino et al., 2015; Thomas et al., 2018). Therefore, in line with current literature, we can suggest that actors' movement kinematics and intentions may be coded by the observer's motor system at different hierarchical levels of action representation (Finisguerra et al., 2018), from the simple prediction of motor output to the deep comprehension of the intentional meaning behind it. Importantly, the involvement of motor simulation seems more pronounced with increased experience. On the one hand, generalized experience (e.g. visual strategies, attention allocation and cue utilization) could complementarily contribute to action recognition, including deceptive movements (Güldenpenning et al., 2017) and social interaction (Koban and

Pourtois, 2014). On the other hand, specific sensorimotor skills endow subjects with a top-down modulation relying on AON that might influence the low-level representation of actions when the observed movement disconfirms the temporal expectation triggered by a specific context. This may corroborate the hypothesis that somatosensory and motor skills of experts exceed the domain of individual motor control and may provide the brain with fine anticipatory, simulative error monitoring systems for the evaluation of others' movements (Candidi et al., 2014; Amoruso and Urgesi, 2016).

The present work has some limitations that should be acknowledged. First, the study does not make use of gaze tracking methods, which has been recently used in combination with TMS to examine the relationship between point of gaze and motor resonance (D'Innocenzo et al., 2017), and could be useful to monitor the strategies adopted by the two groups during AO. A second drawback of the present study is the lack of a control muscle in the TMS experiment, which could help disambiguate which aspects of the observed action modulated M1 in soccer players.

Conclusions

In conclusion, action prediction ability seems to be independent of individual motor repertoire, allowing both skilled subjects and novices to infer the correct timing of an observed action. By contrast, only subjects with previously acquired sensorimotor skills seem to be able to attribute an intentional meaning to the movement of others. In this population, the selective modulation of M1 excitability suggests that action understanding is based on motor resonance and is linked to the ability to discriminate when an action is plausible with respect to the context.

Conflict of interest

None declared.

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